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THE STRUCTURE OF THE CHOANAE OF THE EMYDINAE (TESTUDINES, TESTUDINIDAE)

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No. 4 — *The Structure of the Choanae of the Emydinae (Testudines, Testudinidae)*

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INTRODUCTION

A variety of ridges, flaps, and papillae are found along the lateral margin of the choanae in many turtles although apparently they have been described only in the Cheloniidae (see Parsons, 1958, for a discussion of that family). The present study describes their occurrence and variation in the Emydinae and comments on the relation of these findings to the phylogeny of this group.

Originally, it was hoped that some account of the histology of emydine choanal papillae and a discussion of their possible functions could be included. However a rather quick check of the former showed that a careful study using special techniques would be necessary before any valuable conclusions could be reached. The gross morphology gives no positive clues to the function of the various structures described below. On the negative side, the flap which is frequently present is almost certainly not a valve between the nasal and oral cavities since it is almost never large enough to close off the entire choanal opening (two specimens of *Pseudemys floridana,* out of sixty-nine seen, are the only possible exceptions). A detailed histological study of this area would thus be a very valuable contribution towards an understanding of the choanal flaps and papillae.

No attempt was made to survey the choanae of the other subfamilies of the Testudinidae although several testudinines were observed. Some variation was observed, but it does not appear to be as great as in the Emydinae. In none of the eight specimens seen, which represent the genera *Chersina, Geochelone, Gopherus, Kinixys,* and *Malacochersus* (terminology that of Loveridge and Williams, 1957), was a papilla found, although the other conditions found in emydines were present.

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the collections under their care: Mr. C. M. Bogert and Dr. S. B. McDowell (American Museum of Natural History), Dr. E. E. Williams (Museum of Comparative Zoology), Dr. D. M. Cochran (United States National Museum), and Drs. N. E. Hartweg and R. E. Etheridge (University of Michigan Museum of Zoology). Dr. McDowell also provided a sketch of the choanae of *Pseudemys scripta hiltoni* and checked several specimens for me, and Dr. Hartweg very kindly examined several specimens of *Pseudemys*. The discussion owes much to the many helpful comments and suggestions of Dr. Williams who has also critically read the manuscript for me. Thanks are also due to Dr. M. C. Parsons who made the drawings and the histological preparations.

OBSERVATIONS

Before presenting the findings of this study, several qualifications and warnings are necessary. First, the sample used, while quite large, is not really adequate either in respect to the number of forms or the number of examples of each form. Representatives of all but two of the genera (*Annamemys* and *Batagur*)[1] and of approximately three-quarters of the recognized species and forms (104 out of 137) were seen. However, the sample was five or more for only thirty-four of these forms, and in thirty-seven cases only one specimen was available. Little effort was made to check the identifications of the specimens, so it is quite possible that some of them are misidentified. The condition of the specimens was frequently not ideal for this study; in some cases the mouth was only partly open and the choanae difficult to see, and in others the preservation of the area was not good. A final problem is that the categories used, which are described below, are arbitrary and not, in all cases, sharply distinct. Thus any future study will almost certainly uncover errors in the present work, especially concerning those forms only one specimen of which was checked.

For descriptive purposes it is convenient to recognize four somewhat arbitrarily separated morphological configurations of the lateral margin of the choana. In the most complex of the four, there is a flap (rarely a ridge) of variable size attached along the lateral choanal margin; near the anterior end of the flap there is a single, generally rather small papilla (see Figs.

[1]The nomenclature used throughout is that of Mertens and Wermuth (1955), except that *Emys* is here considered to be monotypic (*E. orbicularis*), with *E. blandingii* being placed in the genus *Emydoidea* as suggested by Loveridge and Williams (1957), and *Hardella indi* is recognized as a valid species.

1 A and B). In most, but not all, specimens possessing such a papilla, the flap is folded ventrally so that it lies along the lateral margin of the choana rather than projecting medially into the opening. A second pattern resembles that described above in possessing a lateral flap, but there is no papilla (see Figs. 1 C and D). The flap is generally slightly smaller than in the first type and usually projects medially into the choana although it is sometimes folded ventrally. In the third group the lateral

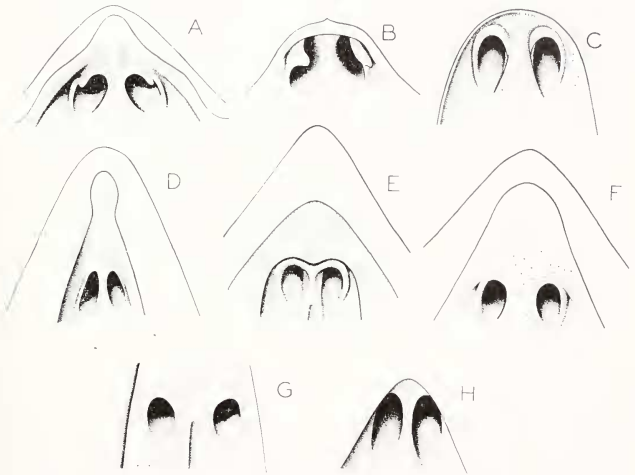

Fig. 1. The choanae of various emydines seen in ventral view to show the four patterns described in the text. The entire palate is not shown. In B, the papilla is folded ventrally on the right side as in the actual specimen; it is shown extended medially on the left. A: *Cyclemys dentata* (MCZ 29573). B: *Hardella thurjii* (MCZ 4002). C: *Hieremys annandalii* (MCZ 4103). D: *Graptemys kohnii* (MCZ 29091). E: *Terrapene ornata* (MCZ 32395). F: *Clemmys marmorata* (MCZ 7877). G: *Malayemys subtrijuga* (MCZ 43083). H: *Graptemys barbouri* (MCZ 46255).

margin of the choana is marked by a ridge rather than a flap (see Figs. 1 E and F); the distinction between a ridge and a flap is quite subjective and, in many cases, the structure could equally well be called either one. In the figures almost no difference is visible, but probing of the actual specimens does reveal

some degree of distinctness. The ridge may project either medially or ventrally. Finally, in the fourth type there is no special structure along the lateral border of the choana (see Figs. 1 G and H). Thus the four patterns may be characterized by the presence, respectively, of a papilla, of a flap, of a ridge, or of nothing at the lateral choanal margin.

The distribution of these four patterns is shown in the following list. The number after each form gives the number of specimens which have been seen, and the letters refer to the patterns, with A for the possession of a papilla, B for a flap, C for a ridge, and D for the absence of such structures. A capital letter is used for the predominant condition while lower case letters indicate less common or variant patterns which were observed.

Callagur borneoensis (1)	A			
Chinemys reevesii (6)		B	c	
Chrysemys picta picta (12)		B	c	
Chrysemys picta bellii (8)		B	c	d
Chrysemys picta dorsalis (1)		B		
Chrysemys picta marginata (2)		B		
Clemmys bealei (1)			C	
Clemmys caspica caspica (2)			C	
Clemmys caspica rivulata (3)		b	C	
Clemmys guttata (15)		b	C	d
Clemmys insculpta (8)		B	c	
Clemmys japonica (1)		B		
Clemmys leprosa (2)		b	C	
Clemmys marmorata marmorata (3)			C	
Clemmys marmorata pallida (8)		b	C	
Clemmys muhlenbergii (6)		b	C	d
Clemmys nigricans (2)			C	
Cuora amboinensis (4)		B		
Cuora flavomarginata (1)		b	C	
Cuora trifasciata (2)		B		
Cyclemys dentata (5)	A			
Deirochelys reticularia (8)			C	d
Emydoidea blandingii (4)		b	C	d
Emys orbicularis (6)			C	d
Geoclemys hamiltonii (1)	A			
Geoemyda annulata (10)		b	C	d
Geoemyda areolata (2)			C	
Geoemyda funerea (3)	A			
Geoemyda pulcherrima pulcherrima (4)		B	c	

Geoemyda pulcherrima incisa (5)		B		
Geoemyda punctularia punctularia (7)	A	b		
Geoemyda punctularia diademata (1)	A			
Geoemyda punctularia lunata (1)	A			
Geoemyda punctularia melanosterna (1)	A			
Geoemyda rubida perixantha (1)			C	
Geoemyda spengleri japonica (2)			C	
Goemyda spinosa (1)				D
Geoemyda tcheponensis (1)	A			
Geoemyda trijuga thermalis (1)			C	
Graptemys barbouri (19)		B	e	d
Graptemys geographica (5)		B	e	
Graptemys kohnii (5)		B		
Graptemys oculifera oculifera (2)		B		
Graptemys oculifera flavimaculata (1)		B		
Graptemys oculifera nigrinoda (2)		B		
Graptemys pseudogeographica pseudogeographica (11)	a	B	e	
Graptemys pseudogeographica ouachitensis (1)		B		
Graptemys pseudogeographica sabinensis (1)		B		
Graptemys pseudogeographica versa (1)		B		
Graptemys pulchra (3)		B		
Hardella indi (1)	A	b		
Hardella thurjii (9)	A			
Hieremys annandalii (1)		B		
Kachuga tecta tecta (2)	A			
Kachuga tecta tentoria (1)[1]	A			
Kachuga trivittata (1)	A			
Malaclemys terrapin terrapin (8)		b	C	d
Malaclemys terrapin centrata (1)			C	
Malaclemys terrapin macrospilota (1)				D
Malaclemys terrapin pileata (3)			C	
Malaclemys terrapin rhizophorarum (2)		B		
Malayemys subtrijuga (2)				D
Morenia ocellata (1)	A			
Notochelys platynota (1)		B		
Ocadia sinensis (3)		B		
Orlitia borneensis (1)		B		
Pseudemys callirostris (1)		B		
Pseudemys dorbigni (1)		B		
Pseudemys floridana floridana (5)	A			
Pseudemys floridana concinna (3)	A			

[1]MCZ 3233; re-identified by Dr. S. B. McDowell.

Pseudemys floridana hieroglyphica (1)	A			
Pseudemys floridana hoyi (7)	A			
Pseudemys floridana mobilensis (18)	A			
Pseudemys floridana peninsularis (13)	A			
Pseudemys floridana suwanniensis (21)	A			
Pseudemys floridana texana (1)	A			
Pseudemys grayi (1)		B		
Pseudemys nelsoni (6)	A			
Pseudemys ornata ornata (2)		B		
Pseudemys ornata cataspila (9)		B	e	
Pseudemys ornata nebulosa (1)	A			
Pseudemys rubiventris rubiventris (24)	A			
Pseudemys rubiventris bangsi (1)	A			
Pseudemys scripta scripta (10)		B		
Pseudemys scripta elegans (16)		B		
Pseudemys scripta gaigeae (2)		B		
Pseudemys scripta hiltoni (4)	a	b		D
Pseudemys terrapen angusta (1)		B		
Pseudemys terrapen decorata (2)		B		
Pseudemys terrapen decussata (29)		B	e	
Pseudemys terrapen felis (1)		B		
Pseudemys terrapen granti (4)		B		
Pseudemys terrapen malonei (6)		B		
Pseudemys terrapen plana (1)		B		
Pseudemys terrapen stejnegeri (2)		B		
Pseudemys terrapen vicina (4)		B		
Siebenrockiella crassicollis (4)		B		
Terrapene carolina carolina (19)		b	C	
Terrapene carolina bauri (3)			C	
Terrapene carolina major (4)			C	
Terrapene carolina triunguis (8)			C	
Terrapene mexicana mexicana (1)			C	
Terrapene nelsoni klauberi (3)			C	
Terrapene ornata ornata (31)			C	

It is obvious from inspection of the preceding list that there are numerous cases in which intraspecific variation occurs. It should also be noted that there can be considerable variation within one of the four categories. The variable forms are here discussed briefly, considering them in alphabetical order by genera.

Chinemys: The variation in *C. reevesii* is primarily the result of the arbitrary distinction between a flap and a ridge; four

specimens have a small flap and two a large ridge, but the difference is very small.

Chrysemys: The possession of a flap is clearly the typical condition in *C. picta;* it occurs in nineteen of the twenty-three specimens. Of the remaining four, three have only a ridge and one has nothing. It is possible, as in all cases in which the variant pattern is essentially a reduction of the normal, that the variant specimens originally showed the typical pattern, but have been damaged or improperly preserved.

Clemmys: This genus seems typically to possess a ridge, but it varies greatly in size, ranging from a small flap to nothing. In most cases this variation is overemphasized by the arbitrary distinction between a flap and a ridge. Four of the five *C. caspica*, three of the eight *C. insculpta*, one of the two *C. leprosa*, and seven of the eleven *C. marmorata* possess a ridge, while the others have a small flap. The variation is greater in *C. guttata* (one with a flap, eleven with a ridge, and three with nothing) and *C. muhlenbergii* (one with a flap, three with a ridge, and two with nothing).

Cuora: The single specimen of *C. flavomarginata* shows a condition almost on the line between a ridge and a flap; despite the fact that the other species of this genus appear to possess a flap, it seems slightly on the ridge side in this one case.

Deirochelys: Five specimens of *D. reticularia* have a very small ridge, while in one there is a larger ridge and in two there is nothing.

Emydoidea: E. blandingii appears to be a rather variable species on the basis of only four specimens; one possesses a flap, two have ridges, and one shows nothing.

Emys: In two specimens of *E. orbicularis* there is nothing, but the other four possess ridges, very faint in one case but well developed in the others.

Geoemyda: This genus shows remarkable variability between species, but the sample seen is too small to permit any detailed consideration of intraspecific variation. Seven of the ten specimens of *G. annulata* possess ridges of variable size while one has a flap and two have nothing. In *G. pulcherrima* there is little actual variation; six specimens have small flaps and two have large ridges. The ninth one has a larger flap. Finally, in *G. punctularia* there is a very small flap which, in nine of the ten specimens, possesses a small papilla.

Graptemys: The possession of a fairly small flap appears to be characteristic of this genus, at least in small specimens. In

G. barbouri a sizable series is available, and there is some variation which seems to be correlated with the size of the animal. The fourteen specimens with a carapace length of less than 120 mm. possess flaps, generally quite small ones, a specimen with a carapace about 120 mm. long has only a ridge, and the four larger ones have nothing. In *G. geographica*, three specimens with carapace lengths of less than 110 mm. have small flaps while ones of 90 and 220 mm. have only ridges. Fourteen specimens of *G. pseudogeographica* with carapace lengths of less than 150 mm. have flaps, while one of two specimens about

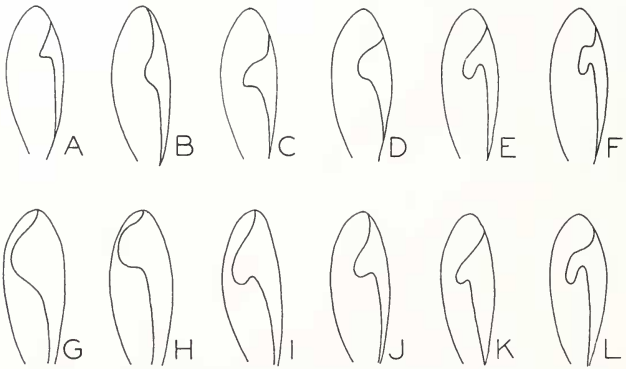

Fig. 2. Outlines of the right choanae of *Pseudemys floridana* to show variation in the size and shape of the flap and papilla. In all cases the flap has been drawn as extended medially. A: *P. f. mobilensis* (MCZ 1662). B: *P. f. suwanniensis* (MCZ 54677). C: *P. f. peninsularis* (MCZ 43849). D: *P. f. peninsularis* (MCZ 43850). E: *P. f. mobilensis* (MCZ 1663). F: *P. f. suwanniensis* (MCZ 43030). G: *P f. mobilensis* (MCZ 1659). H: *P. f. suwanniensis* (MCZ 54667). I: *P. f. hieroglyphica* (MCZ 16487). J: *P. f. suwanniensis* (MCZ 54676). K: *P. f. mobilensis* (MCZ 1651). L: *P. f. mobilensis* (MCZ 1648).

200 mm. long has a flap and the other only a ridge. One of the smaller specimens possesses a small papilla (the only case in fifty-two examples of this genus). All the other species are represented only by small specimens with carapace lengths of under 120 mm.

Hardella: In the one specimen of *H. indi* (kindly examined for me by Dr. McDowell), a papilla was present on one side, but not on the other which had only a flap.

Malaclemys: A ridge is apparently typical of *M. terrapin* and is found in nine of the fifteen specimens; four have small flaps and two show nothing.

Orlitia: In the one specimen of *O. borneensis* (examined by Dr. McDowell), the margin of the flap is slightly scalloped; such a pattern is otherwise unknown among the emydines.

Pseudemys: This genus falls into two main sections, the *P. floridana* plus *P. rubiventris* series, and the *P. scripta* series. All one hundred specimens of the first group (representing all the forms recognized by Mertens and Wermuth, 1955) possess papillae. There is considerable variation in the size of both the flap and the papilla and in the shape of the latter, as is shown in Figure 2. This variation does not appear, on the basis of the

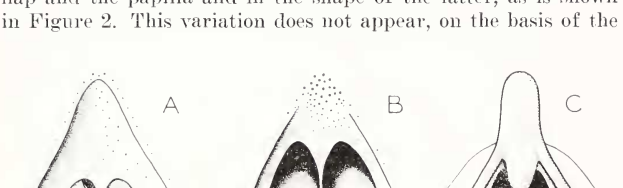

Fig. 3. A: Ventral view of the choanae of an anomalous specimen of *Pseudemys terrapen decussata* (MCZ 56437). B and C: Ventral views of the choanae of two specimens of *Pseudemys scripta hiltoni* to show the variation in this form (B, MCZ 46678; C, AMNH 63748).

sample seen, to be related to either the size of the animal or the race to which it belongs, although *P. rubiventris* may tend to have a slightly smaller flap than *P. floridana.* The *P. scripta* series as a whole is characterized by the possession of a flap of variable and frequently rather small size, but no papilla; such a pattern is found in eighty-nine of the ninety-seven specimens of this series. Two specimens (one *P. ornata catespila* and one *P. terrapen decussata*) have only a ridge, while another *P. terrapen decussata,* shown in Figure 3 A, presents a completely anomalous picture. In the last specimen, the entire choana is covered by a thin membrane pierced on one side by two small circular openings and on the other side by a single such hole. Finally, *P. ornata nebulosa* and *P. scripta hiltoni* do not follow the pattern set by the remainder of the series. In the type and

only example of the former used in the present study (kindly examined for me by Dr. Hartweg), there is a papilla present. Two of the four specimens of *P. scripta hiltoni* also possess papillae, on both sides in one case and on only one side in the other, while the other two specimens (including the type examined by Dr. Hartweg) have no sign of any special structure along the lateral choanal margin (see Figs. 3 B and C). The degree of variation seen in this form is thus greater than that found in any other emydine examined.

Terrapene: All the species of this genus typically have a ridge which varies greatly in size in all cases where there is an adequate sample. Two of the thirty-four specimens of *T. carolina* possess small flaps and are the only exceptions. In *T. ornata,* five of the thirty-one specimens have a small bump near the anterior end of the ridge; it does not closely resemble the papillae found in other genera and is probably an independent specialization. However it could be a vestigial papilla.

DISCUSSION

This discussion deals primarily with the phylogenetic implications of the various choanal structures described above. It must, of course, be emphasized that no one character can ever provide a reliable basis for any phylogenetic scheme; many different and unrelated characters must be considered. However, such a detailed treatment is beyond the scope of this paper, and the following remarks can be no more than suggestive. An added liability is that, of necessity, only living forms are treated so that dendrograms rather than true phyletic trees must be used. In considering the relationships between genera, Williams' dendrogram of the emydines (Loveridge and Williams, 1957, p. 185) forms the most convenient starting point. It is reproduced as Figure 4 with the various symbols that he used for different characters omitted, but with the choanal configurations noted after each genus in parentheses. The letters used are the same as those in the list in the descriptive section (A for papilla present, B for flap, C for ridge, and D for nothing). Only what is believed to be the typical pattern or patterns is indicated; rarer variants are omitted.

The first problem to be faced is the determination of which choanal configuration is to be considered most primitive, and which specialized. In the absence of any knowledge of the functional significance of the various structures, this is not easy and

the conclusions cannot be considered absolutely reliable. The lack of any *obvious* function suggests that the most complex pattern, that of a papilla plus flap, may be primitive, and that the evolutionary picture within the emydines is one of loss,

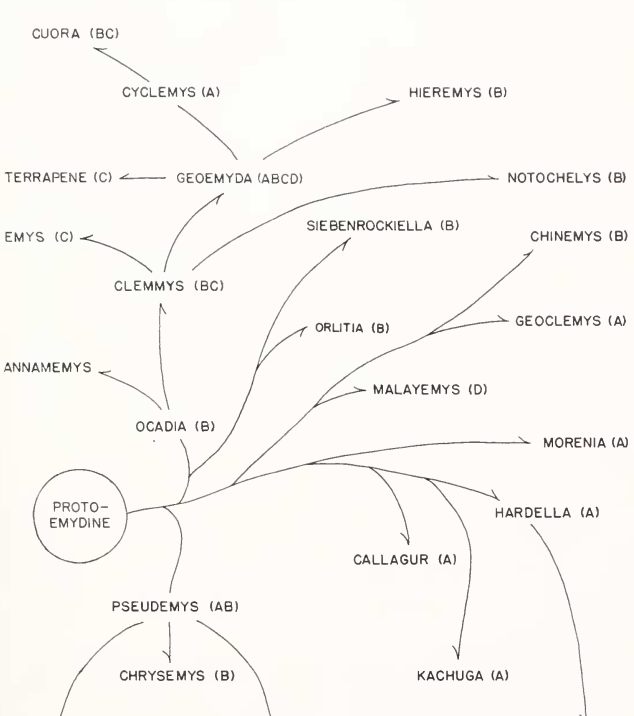

Fig. 4. Dendrogram of emydine relationships (modified from Loveridge and Williams, 1957). The letters in parentheses indicate the choanal configurations typical of the various genera, with A for the presence of a papilla, B for a flap, C for a ridge, and D for nothing.

occurring at different rates and in different groups of related genera. If the reverse is assumed, that the papilla is a specialized structure evolved within certain emydines, then the diversity of the forms in which it occurs appears to require that it has evolved in parallel fashion in several lines. While such a parallel development is certainly possible, its acceptance is somewhat embarrassing in the absence of any functional explanation.

A more profitable way to attack the problem is to see which choanal pattern is found in those genera previously thought to be primitive. However, the results again cannot be considered conclusive; the primitiveness of one structure in an animal is no proof that another structure in that animal is also primitive. As shown in Figure 4, the unicarinate series (*Pseudemys* and allies) fits in well with the theory that the presence of a papilla is primitive. However, in the remaining forms (the tricarinate series), no pattern is discernible. One subgroup, the Asian river turtles (*Callagur* and allies), consistently possesses a choanal papilla (*Hardella indi* is a minor exception); while these forms do show certain characters which Williams considered to be primitive, they have exaggerated such traits (strong buttressing of the shell, wide triturating surfaces, and maxillary triturating ridges) to an extreme and presumably quite specialized condition. The other subgroups are less consistent and hence harder to discuss. One interesting point can be noted: the genera showing the smallest development of choanal papillae or flaps are almost certainly *not* primitive. The only genus characterized by the total absence of any choanal structure, *Malayemys*, has a very specialized skull with a well developed secondary palate and no waist to the united pterygoids. *Terrapene* and *Emys*, which have only a ridge, both possess a hinged plastron which is certainly not a primitive trait.

Hence it seems most probable that the primitive emydine possessed a well developed choanal flap with a papilla, but that this has been reduced to a greater or lesser degree in many of the Recent genera. Such will be assumed, despite its unproven nature, throughout the remainder of the discussion.

As stated above, if the presence of a papilla is considered primitive, the unicarinate series of genera (*Pseudemys* and allies) shows a consistent pattern of simplification in Williams' dendrogram, so that the nature of the choanae may be used as additional evidence for his views. Two of the subgroups of the tricarinate assemblage are uniform and hence this character is of no use in a study of their relationships: all of the Asian river

turtles (*Callagur* and allies) seen in the present study possess a papilla, and both *Orlitia* and *Siebenrockiella* have a flap. In the latter case the irregularity of the margin of the flap in *Orlitia* appears to be a specialization, but it is a very minor one and probably cannot be used to deny the more primitive nature of that genus (the characters in which it is shown as more primitive than *Siebenrockiella*, by Williams, are the presence of moderate buttressing of the shell, the presence of ridges on the maxillary triturating surface, and the position of the humeropectoral suture).

The other subgroups are more complex and present definite problems. In the case of *Malayemys*, *Geoclemys*, and *Chinemys*, I believe that the choanal structures probably reflect the true order of specialization, with *Geoclemys* most primitive and *Malayemys* most advanced. This belief is based on an examination of the skulls of all three forms (in the case of *Geoclemys* drawings of the skull kindly furnished by Dr. McDowell were also used to advantage). The following are the specializations noted within these genera: enlargement of the maxillary triturating surface (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter); straightening of the lateral margin of the pterygoid with a reduction of the waist of the united pterygoids (least in *Chinemys* and most in *Malayemys* with *Geoclemys* closer to the former); reduction of the ventral projection of the articular process of the quadrate (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); reduction of the interorbital fenestra (least in *Chinemys* and most in *Malayemys* with *Geoclemys* closer to the former); reduction of the orbitonasal foramen (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter); narrowing of the incisura columellae auris (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); enlargement of the mandibular triturating surface (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the former); and enlargement of the coronoid process (least in *Geoclemys* and most in *Malayemys* with *Chinemys* closer to the latter). In Williams' dendrogram, the only characters in which these three genera are noted as differing are in the position of the humeropectoral suture, which crosses the entoplastron only in *Chinemys*, and in the partial loss of the tricarinate pattern in *Chinemys;* in both these cases *Chinemys* is considered to be more specialized than the other two genera.

A larger and more difficult subgroup is that containing *Ocadia*, *Clemmys*, and their allies. Here the pattern of choanal types appears to be nearly random. *Ocadia* is unique in this subgroup in the possession of two characters considered by Williams to be primitive: moderate buttressing of the shell and ridging of the maxillary triturating surface. Possibly this form and *Annamemys* should be removed from the base of the larger subgroup and made into another small independent subgroup. However, such a suggestion would have to be substantiated by the study of other characters before it could be proposed with any confidence, especially since Williams' diagram is a dendrogram and not a true phyletic tree; the Recent *Ocadia sinensis* is certainly *not* ancestral to the whole assemblage of genera. The other problem within this subgroup concerns the position of *Geoemyda*. This genus is exceedingly variable, with different species showing all four types of choanal structure. If *Geoemyda* were to be considered more primitive with *Clemmys* descended from it rather than the reverse, then the remainder of the subgroup would present a consistent pattern. However, especially in view of the trend towards reduction or loss of the temporal arcade in *Geoemyda*, this certainly cannot be more than suggested as one possibility on the evidence given in this paper. Further discussion of this subgroup without the consideration of numerous other characters does not appear to me to be profitable and is, therefore, not attempted.

Finally, the situation within the genus *Pseudemys* deserves some comment. The *P. floridana* plus *P. rubiventris* series always possess a choanal papilla and hence are presumably primitive. In the *P. scripta* series only a flap is present typically; the only significant exceptions are in populations found in western Mexico (the other three exceptions, two specimens with ridges and one anomalous case, can hardly be considered significant). I have not seen any *P. ornata nebulosa*, but the type was checked by Dr. Hartweg and found to possess a papilla. Papillae are also present in two of the four specimens of the type series of *P. scripta hiltoni* (the specific distinction of *P. ornata* and *scripta* is open to serious doubt; see Williams, 1956). These data obviously suggest that these forms may be the most primitive of the *scripta* series. However, the situation is not simple; *hiltoni* varies greatly, and in two of the specimens (including the type) there is no trace of any papilla, flap, or ridge along the lateral choanal margin. One possible theory is that *nebulosa* is primitive and that *hiltoni* represents an intergrade population between

nebulosa and *P. scripta gaigeae*. Under such conditions the great variation seen in *hiltoni* would not be too surprising. Unfortunately, not only is my sample of these forms small, but the total knowledge of *hiltoni* is minimal and whether or not it actually does intergrade with other forms is completely unknown.

The most recent survey of the entire *scripta* series is that by Williams (1956). He used plastral pattern as a primary character. Based on this, he recognized three subseries, one (*scripta*) in the United States, a second (*ornata*) in Mexico, Central and South America, and the West Indies, and a third ("intermediate populations") in northern and western Mexico. He further suggested that the *ornata* subseries may be the most primitive since its plastral pattern resembles that of the *P. floridana* series plus species in certain closely related genera. Both *hiltoni* and *nebulosa* have patterns not closely comparable with those of the remaining forms although they may, in certain cases at least, resemble each other. Although the plastral pattern of the type of *hiltoni* is quite distinctive, there is considerable variation in the type series (four specimens; see Carr, 1942), and definite statements on the affinities of this form do not appear to be possible. Thus, while the evidence of choanal structure and that of plastral patterns seems to be somewhat at variance, both would indicate a close relationship between *hiltoni* and *nebulosa*. Beyond that, definite conclusions cannot safely be drawn.

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